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MAcroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions

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Abstract

Macroecology is the study of patterns, and the processes that determine those patterns, in the distribution and abundance of organisms at large scales, whether they be spatial (from hundreds of kilometres to global), temporal (from decades to centuries), and organismal (numbers of species or higher taxa). In the context of invasion ecology, macroecological studies include, for example, analyses of the richness, diversity, distribution, and abundance of alien species in regional floras and faunas, spatio-temporal dynamics of alien species across regions, and cross-taxonomic analyses of species traits among comparable

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native and alien species pools. However, macroecological studies aiming to explain and predict plant and animal naturalisations and invasions, and the resulting impacts, have, to date, rarely considered the joint effects of species traits, environment, and socioeconomic characteristics. To address this, we present the MAcroecological Framework for Invasive Aliens (MAFIA). The MAFIA explains the invasion phenomenon using three interacting classes of factors – alien species traits, location characteristics, and factors related to introduction events – and explicitly maps these interactions onto the invasion sequence from transport to naturalisation to invasion. The framework therefore helps both to identify how anthropogenic effects interact with species traits and environmental characteristics to determine observed patterns in alien distribution, abundance, and richness; and to clarify why neglecting anthropogenic effects can generate spurious conclusions. Event-related factors include propagule pressure, colonisation pressure, and residence time that are important for mediating the outcome of invasion processes. However, because of context dependence, they can bias analyses, for example those that seek to elucidate the role of alien species traits. In the same vein, failure to recognise and explicitly incorporate interactions among the main factors impedes our understanding of which macroecological invasion patterns are shaped by the environment, and of the importance of interactions between the species and their environment. The MAFIA is based largely on insights from studies of plants and birds, but we believe it can be applied to all taxa, and hope that it will stimulate comparative research on other groups and environments. By making the biases in macroecological analyses of biological invasions explicit, the MAFIA offers an opportunity to guide assessments of the context dependence of invasions at broad geographical scales.

Keywords

climate, colonisation pressure, geographic range, habitats, invasion stages, non-native, propagule pressure, residence time, species traits, vertebrates

Introduction

Macroecology as a tool to study biological invasions

Invasive alien species introduced by humans to areas beyond their native distributions (Richardson et al. 2000; Blackburn et al. 2011) are a major threat to the world's biodiversity and economy (McGeoch et al. 2010; Blackburn et al. 2014; Brondizio et al. 2019; Pyšek et al. 2020). The numbers of alien species (and the subset of them that are invasive) are increasing rapidly world-wide and there is no sign of deceleration (Hulme et al. 2009; Seebens et al. 2017, 2018). Ongoing globalisation (Perrings et al. 2010), increasing levels of ecosystem modification, and climate warming (Walther et al. 2009) are expected further to accelerate alien species introductions, naturalisations and impacts (Essl et al. 2011a; Hulme 2017; Haeuser et al. 2018).

Research in invasion science over the last 30 years has focussed on questions aimed at improving predictions about which species will form invasive populations, and where these will occur (Drake et al. 1989; Rejmánek 2000; Kolar and Lodge 2002; Pyšek and Richardson 2007). These questions were motivated by the desire to prevent and mitigate the multiple environmental and socioeconomic impacts of alien species. This body of research has given us a better understanding of the importance of context dependence in biological invasions (Sapsford et al. 2020) and of the interactions

among the multiple key drivers that influence the outcome of invasion (e.g. Higgins and Richardson 1998; Simberloff and von Holle 1999; Blumenthal 2006; Sol et al. 2008b; Pyšek et al. 2009a, 2015). This complexity is now fully appreciated and has been addressed by the development of numerous hypotheses and concepts (Catford et al. 2009; Enders et al. 2018, 2020; Jeschke and Heger 2018), theoretical frameworks (e.g. van Kleunen et al. 2010a; Gurevitch et al. 2011; Strayer 2012; Hulme et al. 2020; Wilson et al. 2020) and statistical models of macroecological patterns (e.g. Rouget and Richardson 2003; Thuiller et al. 2006; Wilson et al. 2007; Küster et al. 2008, 2010; Pyšek et al. 2009a, b, 2015; Castro-Díez et al. 2011; Schmidt and Drake 2011; Dawson et al. 2017; Essl et al. 2019). Since multiple factors determine invasion success and impacts, invasions can only be understood in the specific context in which they occur (Novoa et al. 2020; Sapsford et al. 2020). For this reason, studies need to be designed to consider the roles of these multiple factors to ensure that meaningful interpretations of outcomes can be made.

Given that thousands of alien species have established populations and spread across previously unoccupied environments, we are now in a position to (and indeed urgently need to) develop an understanding of the macroecological processes that underpin biological invasions. Macroecology is the study of large-scale (i.e. from hundreds of square kilometres to global in terms of space; from decades to centuries in time; and for large numbers of species or a broad range of taxonomic groups) patterns in the distribution and abundance of species, and the processes that determine those patterns (Gaston and Blackburn 2000; McGill 2019). To qualify as macroecological, a study needs to meet the scale requirement in at least one dimension; in invasion science, it is rare that studies conform to this definition in all three dimensions (but see Seebens et al. 2017, 2018) as can be inferred from the overview of studies presented in Appendix I.

Macroecology seeks to identify generality in complex ecological systems through comparative study of their properties, such as species assemblages or geographic ranges; it therefore addresses issues such as spatial and temporal variation in species richness, interspecific variation in abundance and range size, and how biological and environmental properties influence these aggregate entities (McGill 2019). For biological invasions, exploring macroecological patterns in the invaded range is a natural extension of research aiming to understand why some aliens become abundant and widespread while others do not, and why some sites accrue more alien species than others.

Attempts to associate biological traits and environmental characteristics with broad-scale patterns in the distribution, abundance, and richness of alien species have built on decades of macroecological research on native species. The assumption underlying this approach is that the ecologies of alien and native populations will be determined by the same drivers, albeit not necessarily in exactly the same way. For example, physiological tolerances of individuals to temperature or precipitation in the native range can be retained for many species in the alien range and climatic niche shifts are quite rare among terrestrial plant invaders (Petitpierre et al. 2012, but see Hulme and Barrett 2013; Early and Sax 2014; Atwater et al. 2018; Datta et al. 2019). Similarly, unless species' life histories change when they move to a new range, effects of these

Table 1. Summary of 102 studies addressing macroecological patterns in biological invasions, with respect to the factors that are studied. Only studies meeting at least one of the following criteria were selected: address a large scale in terms of space (from hundreds of square kilometres to global), time (from decades to centuries) or taxonomy (for large numbers of species or a broad range of taxonomic groups). See Appendix I for the list of studies on which these statistics are based. Only six studies (5.9% of the total examined) considered all but one of the seven factors distinguished, 10 studies (9.9%) explored the effect of five factors, and 13 (12.9%) addressed four factors. The vast majority of studies (72, i.e. 71.3%) considered three factors or fewer.

		Factors investigated						
Number of papers	Number of factors studied in combination	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages
0	7							
2	6	×	×	×	×	×		×
2	6	×	×	×	×	×	×	
1	6	×	×	×	×		×	×
1	6	×	×		×	×	×	×
4	5	×	×	×	×		×	
2	5	×	×	×		×		×
1	5	×	×	×		×	×	
1	5	×		×	×		×	×
1	5	×	×			×	×	×
1	5		×	×	×	×		×
2	4	×	×			×		×
2	4	×	×		×	×		
2	4	×	×			×	×	
1	4	×	×	×	×			
1	4	×		×		×		×
1	4	×		×	×			×
1	4	×				×	×	×
1	4	×			×	×	×	
6	3	×				×		×
4	3	×		×		×		
3	3	×	×	×				
3	3	×	×					×
2	3	×	×		×			
2	3	×		×	×			
2	3		×	×		×		
1	3	×		×				×
1	3	×		×			×	
1	3	×	×			×		
1	3	×			×			×
8	2	×		×				
6	2	×						×
3	2	×	×					
2	2	×				×		
2	2	×			×			
1	2	×					×	
1	2		×	×				
1	2				×	×		
1	2				×			×
19	1	×						
1	1			×				
1	1					×		
102		93	40	41	27	37	19	34

traits on macroecological patterns in the native range should be maintained in the alien range. Plant species that are good competitors should retain this ability in the invaded range; some will become even better competitors due to enemy release (e.g. Keane and Crawley 2002), and some will become invaders by behaving in the same way as in their native range (Firn et al. 2011; Parker et al. 2013; Colautti et al. 2014).

The assumption that the ecologies of alien and native populations will be determined by the same drivers might not hold if the traits of conspecific individuals in the alien and native populations differ, e.g. due to founder effects, or evolution, or if resource limitation differs, e.g. when species move from an N-limited to a light-limited system. However, and more fundamentally, the identity and location of alien populations are determined by human activities, in a manner that is of a different order and type to that for native populations (Wilson et al. 2009). Thus, while human activities undoubtedly profoundly affect macroecological patterns in native populations (e.g., Gaston and Blackburn 2003; Faurby and Araújo 2017), the macroecological patterns and processes of alien populations are more strongly mediated by anthropogenic influences (Richardson et al. 2000; Blackburn et al. 2011). For example, similar factors seem to influence the native and alien range sizes of pine species (Richardson and Bond 1991), but alien range sizes are additionally profoundly influenced by anthropogenic factors (McGregor et al. 2012; Procheş et al. 2012).

Context dependence in biological invasions: evidence from literature

With respect to alien abundance and distribution, a growing literature shows that some species traits are generally associated with the capacity to form self-sustaining populations that spread from points of introduction (i.e. invasive *sensu* Pyšek and Richardson 2007; van Kleunen et al. 2010b). For example, Pyšek et al. (2009a, 2015) used a source-area approach (as defined by Pyšek et al. 2004b) to show that the success of Central-European plant species introduced to other areas of the world results from the interaction of their distribution in the native range, habitats they occupy there, their biological traits, propagule pressure as a consequence of human use, and residence time. Jeschke and Strayer (2006) showed that invasiveness was related to native range size for mammals, birds and freshwater fish alien to Europe and North America. Recent studies revealed that fast life-history strategies, that allow for rapid increase in population size, characterise successful alien mammals (Capellini et al. 2015), reptiles (Allen et al. 2017) and plants (Richardson and Rejmánek 2004; van Kleunen et al. 2010b), while alien birds rather adopt slow strategies (Sol et al. 2012). In birds and mammals, a generalist life-style characterised by behavioural flexibility and larger trait variation is associated with successful establishment (Sol et al. 2008a, 2012; González-Suárez et al. 2015), while in insects specialised species seem to be more successful (Rossinelli and Bacher 2015). At the global scale, Dyer et al. (2016) showed that variation in the alien geographic range size of birds was positively associated with native geographic range size, while there was no effect of either body mass or ecological

specialisation controlling for other variables. Environmental factors, including climate and habitat match between source and target regions (Thuiller et al. 2005; Hejda et al. 2009; Kalusová et al. 2013) are also likely to be important for invasiveness. For example, Duncan et al. (2001) showed that alien bird species with larger geographic ranges in Australia had a larger area of climatically suitable habitat on the continent.

For plants, several studies have addressed the role of traits in invasions in concert with other factors codetermining invasiveness (e.g. Herron et al. 2007; van Kleunen and Johnson 2007; Gravuer et al. 2008; Küster et al. 2008), but none of them simultaneously: (i) used a global dataset, (ii) analysed different stages of invasion process, (iii) took characteristics of the native and introduced ranges, such as its size, climate or habitat affiliation, into account together with species traits, and (iv) included the effect of residence time and propagule pressure (Table 1, Appendix I). Thuiller et al. (2006) studied how species traits, characteristics of the native and introduced ranges, residence time, and human usage shape the distribution of invasive alien plant species, but they based their analysis on the invading species pool in the target region of South Africa. Hamilton et al. (2005) analysed the role of several species traits in invasions at different spatial scales but, while they accounted for phylogenetic effects, they did not address different stages of the invasion process, and nor did they consider distributional characteristics in native ranges. Van Kleunen et al. (2007) studied different invasion stages by analysing introduction through horticultural trade and subsequent naturalisation separately, and employed distributional characteristics together with species traits, but only for species within the family Iridaceae. Gravuer et al. (2008) considered human and biogeographic factors as well as traits and three invasion stages, but only for a single genus (i.e. *Trifolium*). Küster et al. (2008) considered distributional characteristics and focused on important interactions among ecological characteristics for one invasion step. Dawson et al. (2009) addressed multiple stages of alien plant invasions for multiple genera in concert with a number of traits, but only for invasions in the tropics. Essl et al. (2011b) explored interactions among native range size, climate match, habitat affiliations, colonisation pressure and propagule pressure, but only for conifer naturalisations. McGregor et al. (2012) examined the role of species traits, biogeographic attributes (including native range size) and human factors on the likelihood of introduction and naturalisation of pine species in separate regions in the Northern and Southern hemispheres.

The need for a formal framework addressing large-scale context dependence in biological invasions

Despite advances in our understanding of invasion dynamics as discussed above, models in the literature that seek to elucidate the determinants of naturalisation and invasion success of alien species from a macroecological perspective (regional to global) rarely include a complete suite of factors that have been acknowledged as key elements in the process (Table 1, Appendix I). Yet, the application of models that analyse multiple

factors in concert to determine their relative importance is crucial to address properly the role of biological traits promoting species invasiveness. Importantly, because of the context dependence of invasions, the real effect of a particular trait can be confounded, for example, if a species possessing a trait is introduced more frequently, or has had a longer time to adapt to, or take advantage of, conditions in the invaded area. Similarly, studies that ignore effects of, for example, habitats in which the species occurs either in the native and/or invaded range may overestimate the role of biological traits, which in turn may result in spurious predictions (Pyšek et al. 2015; Duncan et al. 2019). At the same time, factors interacting with the species traits themselves, such as propagule pressure and residence time, play important roles in determining the outcome of particular invasions.

Here, we develop a formal framework to explore the context dependence of invasions at broad geographical scales, and to increase awareness that macroecological analyses can yield biased results if these issues are ignored. We discuss different aspects of the framework by using examples of previous macroecological studies mostly based on plants and birds, as these two groups have been studied in most detail from this perspective. However, we believe that the framework is applicable to a broad range of taxa, and we hope that it will stimulate comparative research in other groups and environments.

MAcroecological Framework for Invasive Aliens (MAFIA): the rationale

At the core of the MAFIA is the notion that three classes of factors and their interactions explain invasions: (i) alien species traits, (ii) location characteristics, and (iii) factors related to introduction events (Fig. 1). This rationale has been mostly used in the animal invasion literature (e.g. Duncan et al. 2003) but is generally applicable across taxa. Event-related factors include propagule pressure and other human factors (e.g. pathways, and date of introduction that determines the residence time), but also, for example, the season during which the species is introduced (summer, winter). These interactions, with the exception of climate matching (which is often treated as a main factor instead of an interaction), have rarely been considered to date. However, an introduction of an alien species with traits suited to establishment in the local abiotic environment and biotic community, with a sufficiently large founding population size, will still fail if, e.g. the resource availability at the time of introduction is insufficient (i.e. a mismatch of location and event characteristics; Fig. 1). For example, it has been shown that propagule pressure only emerges as a strong predictor of invasion success of pest insects alien to Europe if the interaction with host availability and the degree of climate matching is taken into account (Bacon et al. 2014, see also Duncan 2016). Failure to recognise and explicitly incorporate interactions among the main factors clearly impedes our understanding of which macroecological invasion patterns are shaped by the environment, and of the importance of interactions between the species and their environment.

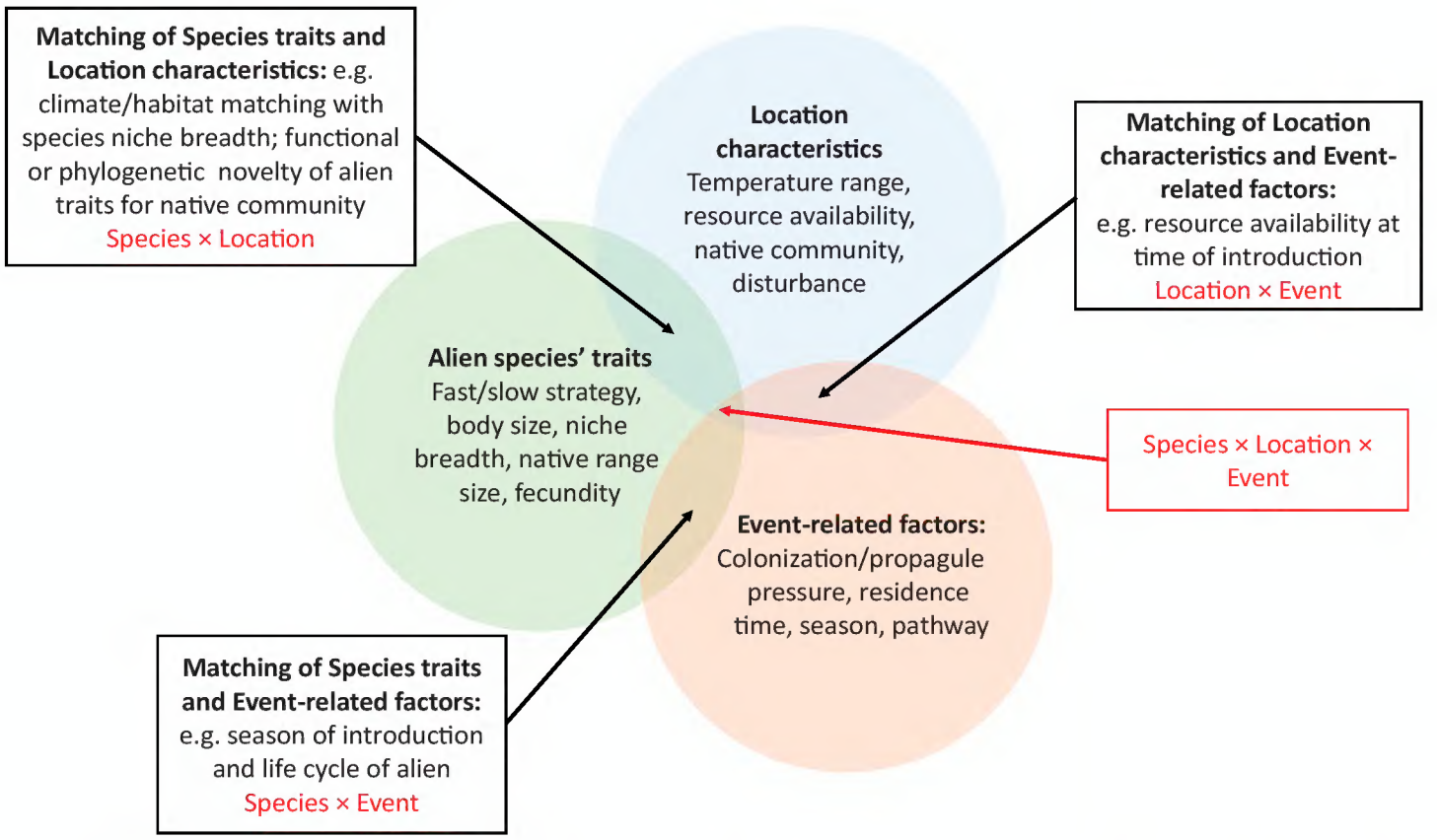
Matching of Species traits and Location characteristics: e.g. climate/habitat matching with species niche breadth; functional or phylogenetic novelty of alien traits for native community
Species × Location
Location characteristics
Temperature range, resource availability, native community, disturbance
Matching of Location characteristics and Event-related factors:
e.g. resource availability at time of introduction
Location × Event
Alien species' traits
Fast/slow strategy, body size, niche breadth, native range size, fecundity
Species × Location × Event
Event-related factors:
Colonization/propagule pressure, residence time, season, pathway
Matching of Species traits and Event-related factors:
e.g. season of introduction and life cycle of alien
Species × Event

Figure 1. A proposed comprehensive typology of factors and their interactions (represented by intersections in the Venn diagram) that explain invasions: Alien species traits, Location characteristics, and Event-related factors. Intersections between two (or all) these main classes of factors denote situations where their combinations determine invasions, e.g. the climate at a location needs to match the niche requirements of the alien to result in a successful invasion. For a successful invasion, all factor classes and their interactions need to be favourable (Species × Location × Event), i.e. a species with suitable traits is introduced to a suitable habitat in a region with matching climate and the propagule numbers arriving during that introduction event are enough to allow for successful establishment, possibly resulting in invasion.

Another key notion is that the macroecological processes of biological invasions are underpinned both by biological and environmental characteristics (that are used to explain the distribution, abundance, and richness of alien species in their native ranges), and by human factors that influence the probability and magnitude of transport and introduction of alien species, and whether, where, and when a species is given the opportunity to succeed. Such human factors include the origin, destination, and means by which species are transported (Sinclair et al. 2020), the locations, identities, numbers of introduction events, numbers of species (colonisation pressure; Lockwood et al. 2009), individuals or propagules (propagule pressure; Lockwood et al. 2005) being introduced, and residence time (Forcella and Wood 1984; Rejmánek 2000; Pyšek and Jarošík 2005; Wilson et al. 2007; Williamson et al. 2009; Gassó et al. 2010), as well as spatial (by widespread dissemination or abundant plantings; Hanspach et al. 2008) and temporal (by long history of cultivation; Rouget and Richardson 2003) variation in these factors.

The awareness of these considerations is at the heart of the MAFIA, depicted in Fig. 2. In macroecological analyses, invasion science aims to explain the occurrence and success of alien species in regional floras and faunas (i.e. their richness, diversity, distribution, abundance, as well as spatial and trait relationships) by using a number of factors related to species traits, and both environmental- and socioeconomic,

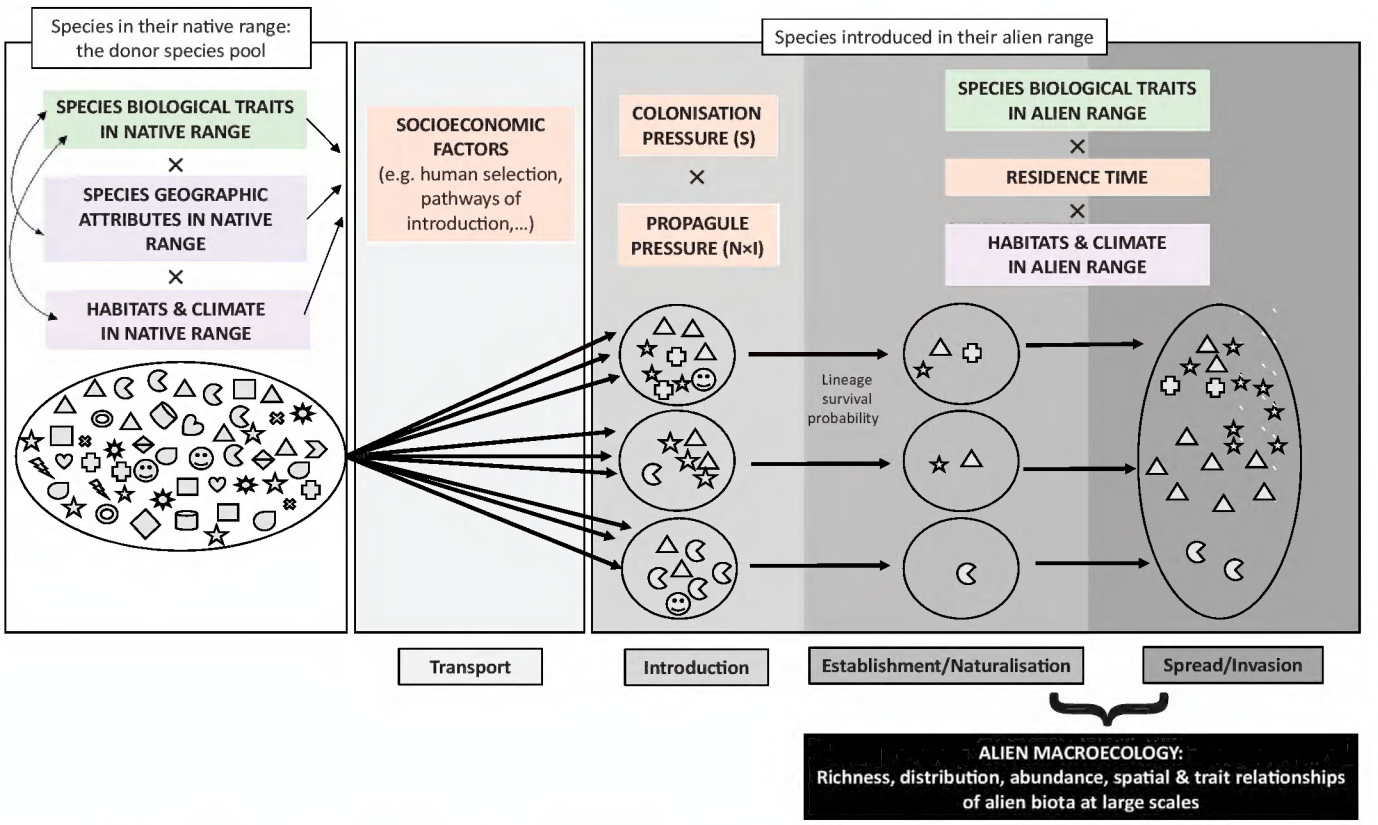

Figure 2. The Macroecological Framework for Invasive Aliens (MAFIA). The classes of factors introduced in Fig. 1 are distinguished by using the same colour codes, i.e. Alien species traits (including their values in the native range) in green, Location characteristics in blue and Event-related factors in orange, and individual factors are shown as operating along the introduction-naturalisation-invasion continuum (INIC). Species geographic attributes and Habitat & Climate in native range are in a different colour (purple) because they influence both Alien species traits and Event-related socioeconomic factors (by influencing the probability that a species will be transported by humans from its native range) but are not directly related to the Location characteristics in introduced range (i.e. to where the species will be introduced). Lineage survival probability is the probability that any one of the introduced individuals leaves a surviving lineage (i.e. founds a population). S, number of species introduced; N, number of individuals introduced per introduction event; I, number of introduction events. See text for explanation.

i.e. human-related, characteristics (Fig. 2). The interaction 'Species biological traits × Geographic attributes × Habitats × Climate × Socioeconomic factors (Introduction pathways and Site/Propagule & Colonisation pressure/Residence time)' needs to be considered in combination to make progress in explaining and predicting plant and animal naturalisation and invasion success, as well as impacts.

Underpinning the MAFIA is the well-established unified framework for biological invasions (Blackburn et al. 2011) and its predecessors for plant (Richardson et al. 2000) and animal invasions (Williamson and Fitter 1996). These frameworks recognise that the invasion process can be conceptualised as a sequence of stages that a species has to pass through to become introduced from its native range and to become alien in the new range, and that each stage acts as a filter that potentially restricts the species that are exposed to each following stage in the sequence (Blackburn et al. 2011; Richardson and Pyšek 2012). The MAFIA thus builds on the introduction-naturalisation-invasion continuum (INIC – Richardson et al. 2011) concept, and some others such as the TEASI framework that formalised the different steps of invasion process based on the notion that factors important at previous steps percolate through to later steps (Leung et al. 2012).

The MAFIA, by explicitly mapping the factors that influence macroecological patterns in alien species onto the invasion pathway, not only helps to identify how anthropogenic effects interact with species traits and environmental characteristics to determine observed patterns in alien distribution, abundance, and richness (amongst other features), but also clarifies why overlooking anthropogenic effects can lead to spurious conclusions. It has been repeatedly shown that different factors influence different stages of the invasion process (Kolar and Lodge 2001; Moodley et al. 2013); socioeconomic factors are suggested to be generally important early in the invasion process, whereas biogeography, ecology, and evolution play more important roles at later stages (Williamson 2006; McGeoch et al. 2016). Thus, if we cannot determine exactly at which stage of the invasion process each analysed taxon is, or if we merge the alien species for analyses regardless of their status (casual, naturalised or invasive; *sensu* Blackburn et al. 2011 and Richardson et al. 2011), it becomes impossible to identify the importance of invasion drivers. Another general problem associated with macroecological analyses is that the quality of data available for large numbers of species comprising whole floras and faunas is often low, and some of the factors thus remain unconsidered (Pyšek et al. 2009a; Gioria et al. 2012, 2019; Kueffer et al. 2013) (Appendix I). The MAFIA recognises that understanding this context is vital to understanding invasion outcomes.

Because of context dependence, the factors mediating the outcome of invasion processes can act to bias some analyses. For example, factors concerning introduction events, e.g. propagule and colonisation pressure (Lockwood et al. 2005; Simberloff 2009) and residence time (Rejmánek 2000; Castro et al. 2005; Pyšek and Jarošík 2005; Williamson et al. 2009; Pyšek et al. 2011), can confound analyses of the effect of alien species traits. Both propagule and colonisation pressure and residence time have fundamental effects on the outcome of invasion (see below) and set the stage upon which the differences in biological traits act in influencing the invasion success of a species (Lonsdale 1999; Colautti et al. 2006; Catford et al. 2009; Fig. 2). However, if the goal is to explore the alien species traits by location interaction (e.g. to assess which types of species tend to become invasive where), it would be inappropriate to compare species with different event characteristics, such as species that were provided with a different periods of time to adapt to the novel environment (residence times) and/or were introduced in different quantities (propagule pressure) (Wilson et al. 2007; Pyšek et al. 2009b, 2015). This is particularly the case if there is covariance between alien species traits and introduction events (e.g. reptiles that are easier to breed are more common in the pet trade; van Wilgen et al. 2010), or covariance between locations and introduction events (e.g. plants tend to be more frequently introduced to lowlands areas than mountains; Alexander et al. 2011).

Elements of the framework

In this section we explore in detail how individual factors captured by the MAFIA, and their interactions, affect the outcome of invasions at the macroecological scale, and what

is the evidence in literature for the role they play. We address these issues along the stages of the invasion process, from transport and introduction to naturalisation and invasion, with discussion on effects of propagule pressure and climate integrated within these sections. The importance of the context brought about by residence time, alien species traits and habitats is discussed in separate sections. For each element of the framework, we indicate to which of the three classes of factors (Figs 1, 2) it is related (Traits – Aliens species traits; Location – Location characteristics; Event – Event-related factors).

Species in their native range: the donor species pool [Traits]

Not all species have alien populations but, in principle, the size of the alien species pool (i.e. alien species richness) can to a large degree be attributed to the size of the donor species pool, dispersal success (incl. human transport, human commensalism and perceived utility) and the fit to the new environment in terms of environmental matching between donor and recipient regions (Karger et al. 2016). It therefore follows that, at the global level, observed aliens are a subsample of the world's native species pool (though exceptions could occur where alien species hybridise and speciate in their new ranges; Ellstrand and Schierenbeck 2000; Levin 2003; Flores-Moreno et al. 2015; Brandenburger et al. 2019). Which species from this pool get entrained on the invasion pathway depends on the interaction of the socioeconomic motivations or determinants for translocation, and the distribution and characteristics of the species (Hulme et al. 2008; Essl et al. 2015; Sinclair et al. 2020). These latter features affect the probability that a species is selected (deliberately or otherwise) for transport. For example, a large native geographic range has been suggested to be among the best determinants of invasion success in seed plants (Rejmánek 1996; Goodwin et al. 1999; Hui et al. 2011), but this factor may affect invasiveness in several ways. First, having a large native range increases the probability of a species being selected for transport (Blackburn and Duncan 2001a) and therefore experiencing high propagule pressure (Cassey et al. 2004c). Second, the traits that allowed the species to achieve a large native range might also allow it to have a large alien range (Booth et al. 2003; Pyšek et al. 2009a; Dyer et al. 2016). Further, a large native range has been proposed to increase the probability that a species will sample a broader range of habitats and becomes better equipped for competition and novel interactions with species in the introduced ranges (Sax and Brown 2000). Nevertheless, this is not true for all taxa. For example, for parrots it has been shown that large geographic range size is a strong predictor of which species are transported outside their native ranges, and which transported species are subsequently introduced, but not which introduced species succeed in establishing (Cassey et al. 2004b); the net result of this, however, is that alien parrots tend to be those with large native ranges.

The biogeographic location of the native range also matters, as not all species pools are equally likely to be sampled for potential aliens. For example, bird species introduced in the 19th and early 20th centuries came primarily from Europe, were

more likely to be introduced to regions of the British Empire, and were more likely to concern species in families of game birds (e.g. pheasants, ducks, and pigeons). These patterns arise because introductions in this period were largely driven by the deliberate activities of Acclimatisation Societies – organisations specifically aimed at promoting introductions of beneficial species, such as game animals, and which were especially active in British colonies (di Castri 1989; Pipek et al. 2015; Dyer et al. 2017).

The relative size and age of species pools in species' native versus alien range also helps to indicate potential evolutionary imbalances (Fridley and Sax 2014). Alien species that have evolved over a longer period of time and in a more competitive and stable environment (e.g. mainland vs islands) tend to have higher competitive ability than co-occurring native species. As plant invasions in the Czech Republic, New Zealand, and eastern North America demonstrate (Fridley and Sax 2014), species from regions with highly diverse evolutionary lineages are more likely to become successful invaders in less diverse regions.

Disentangling the relative roles of species traits and properties of native geographic ranges in the context of anthropogenic effects is thus a fundamental task for invasion science. Knowing the extent to which the characteristics of the native range of a species can explain and predict its invasion, and under what contexts, would improve the precision of prediction systems used in weed-risk assessment (e.g. Pheloung et al. 1999; Weber et al. 2009).

Transport and introduction: socioeconomic factors, propagule pressure, and colonisation pressure [Event]

There are at least three important consequences of the intersection of the socioeconomic motivations for introduction of aliens from the native species pool. First, the identities of introduced species are a non-random subset of all species that could have been introduced (see also Karger et al. 2016; Maurel et al. 2016). This can have significant consequences for our perceptions of the kinds of species that become invasive, and for our interpretation of the resulting macroecological patterns. For example, introduced wildfowl species are larger-bodied, on average, than those wildfowl that have not been introduced (Blackburn and Duncan 2001a). It follows that established wildfowl species are likely also to be large-bodied, and that the macroecological patterns expressed by alien wildfowl will be a consequence of how body size might influence the distribution and abundance of these species. It is important to factor such non-randomness into any analysis of later stages of the invasion process, including macroecological analyses, or incorrect conclusions about processes are likely to be reached (Cassey et al. 2004a; Pyšek et al. 2009a; Hui et al. 2014).

Second, sites to which species are introduced also depend on interactions between introduction pathways and the donor species pool. Again, incorrect conclusions about processes are likely to be reached without factoring in this context, especially as native species are not distributed randomly with respect to evolutionary history or

associated traits, and hence pathway locations and species-pool composition interact. For example, socioeconomic changes in societies around the world have driven changes in the reasons for, and the geographical dimensions of, human-induced movement of bird species (Blackburn et al. 2009; Dyer et al. 2017); the source regions, destinations and identities of introduced species have shifted significantly in recent decades. Bird introductions are now driven largely by the pet trade, especially in rapidly developing economies in the Middle and Far East. This may explain why alien bird species follow Bergmann's rule (Fig. 3), such that the average body mass exhibited by alien bird assemblages decreases toward the equator (Blackburn et al. 2019). Alien bird species appear to follow closely the relationship exhibited by native birds (Olson et al. 2009), but this is to a large extent a consequence of the fact that large-bodied species have been introduced at higher latitudes, on average, than small-bodied species, followed by latitudinal variation in establishment success that is independent of body mass (Blackburn et al. 2019). Historical introductions driven by Acclimatisation Societies tended to prefer large-bodied species and higher latitudes than recent introductions, which tend to be cage bird species such as parrots and estrildid finches, and to occur at lower latitudes (Dyer et al. 2017).

Third, patterns of selection from native species pools along different introduction pathways will affect the numbers of species (colonisation pressure; Lockwood et al. 2009) and individuals (propagule pressure; Lockwood et al. 2005; Simberloff 2009) that are introduced to different locations around the world. Models have shown repeatedly that the random selection of individuals from a species pool with realistic population structure will result in more species, and more individuals per species, in larger samples, as may occur for example in species transported in ballast water (Lockwood et al. 2009). More abundant species are more likely to be transported in this way. The same patterns hold for planned introductions (Cassey et al. 2004c). Variations in the levels of invasion among recipient communities, habitats or regions could be, in some cases, simply due to differences in the numbers of arriving aliens (Williamson 1996).

Lonsdale (1999) and Duncan et al. (2019) showed for plants and birds, respectively, that alien species richness at a location is a function of the number of species introduced to the location and the probability that any given introduced species establishes a viable population. Duncan et al. (2019) further showed that, for a closed system such as an island, establishment in turn is a function of the number of individuals introduced, and the probability that any one of those individuals leaves a surviving lineage (lineage survival probability; Fig. 2). Thus, alien species richness is primarily a consequence of the introduction process, and specifically colonisation and propagule pressures. These anthropogenic effects are fundamental to understanding the invasion process, and must be explicitly considered if the alien macroecological patterns that result are to be interpreted correctly (this is particularly notable early on in the invasion process, e.g. when looking at factors that determine the site of first detections; Huang et al. 2012). As an analogy, attempting to understand the drivers of alien species richness by performing a manipulative experiment in which the number of species added to each treatment was unknown would be unwise. It is similarly difficult to unravel the

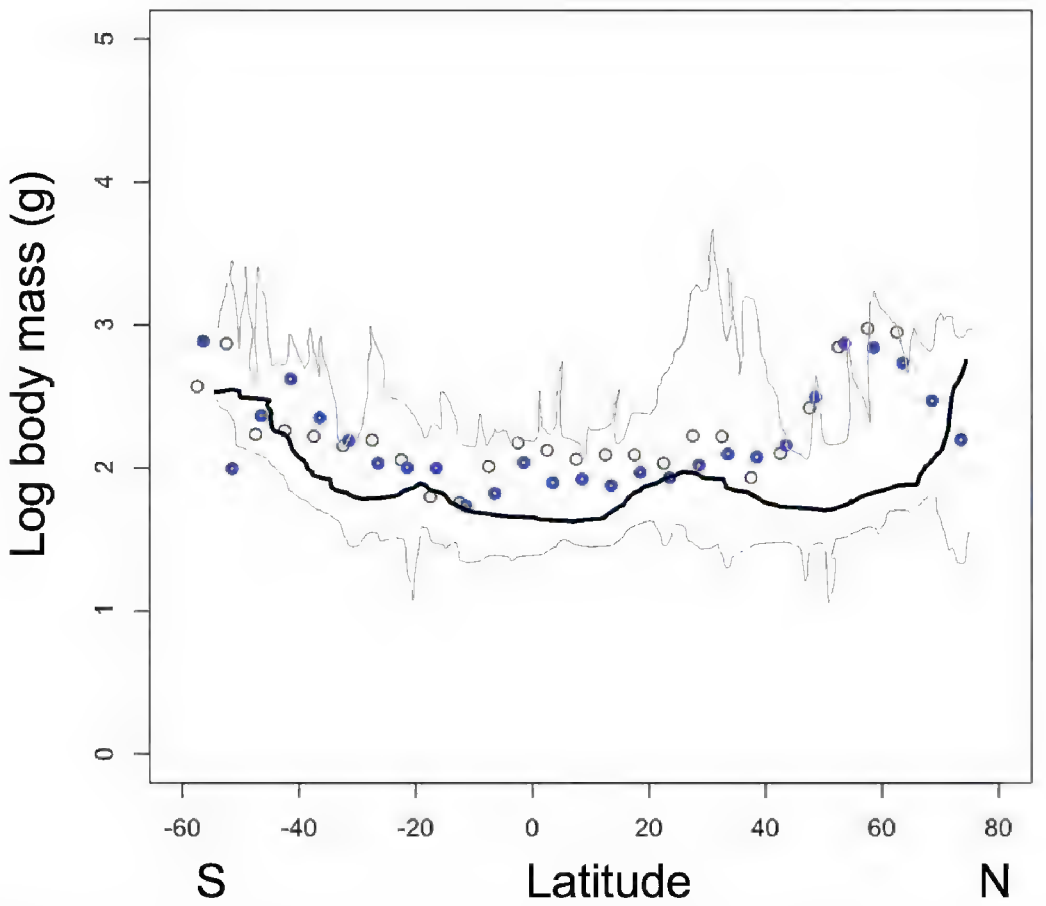

Figure 3. Latitudinal variation in body mass for introduced (black, unfilled circles) and established (blue, filled circles) alien bird species worldwide, together with the mean (thick line) and range (thin line) of the relationship for native bird species. See text for details. Data from Blackburn et al. (2019) and Olson et al. (2009).

drivers of alien species richness in natural experiments where colonisation pressure is unknown. Duncan et al. (2019) carried out simple sensitivity analyses to show that by far the strongest determinant of alien species richness in their model was colonisation pressure; they show that increasing propagule pressure or lineage survival probability will increase alien species richness, but only up to an asymptote imposed by colonisation pressure. All else being equal, increasing colonisation pressure allows alien species richness to continue to grow as a linear function. While this model technically applies to closed systems, and it is not clear whether it applies to all taxa, most alien bird species at least do not spread far from points of introduction (Dyer et al. 2016). The implication is that for birds in most broad locations, colonisation pressure is a much more influential driver of incursion than spread. For many plant invasions, however, new population foci create potent propagule pressure sources that drive invasions much more quickly than the size and other dimensions of the source population, as demonstrated, for example, by the invasion of *Opuntia stricta* in Kruger National Park, South Africa (Foxcroft et al. 2004).

Data on colonisation pressure are rarely available for taxa other than vertebrates (i.e. alien species that were intentionally released outside of captivity, but see also insects released for biocontrol; Rossinelli and Bacher 2015). Quantification of colonisation pressure requires data on the number of species introduced in total, but data on failed invasions are generally scarce (but see Diez et al. 2009). Propagule pressure is also extremely difficult to measure at a large scale for plants (Fig. 4). Therefore, vari-

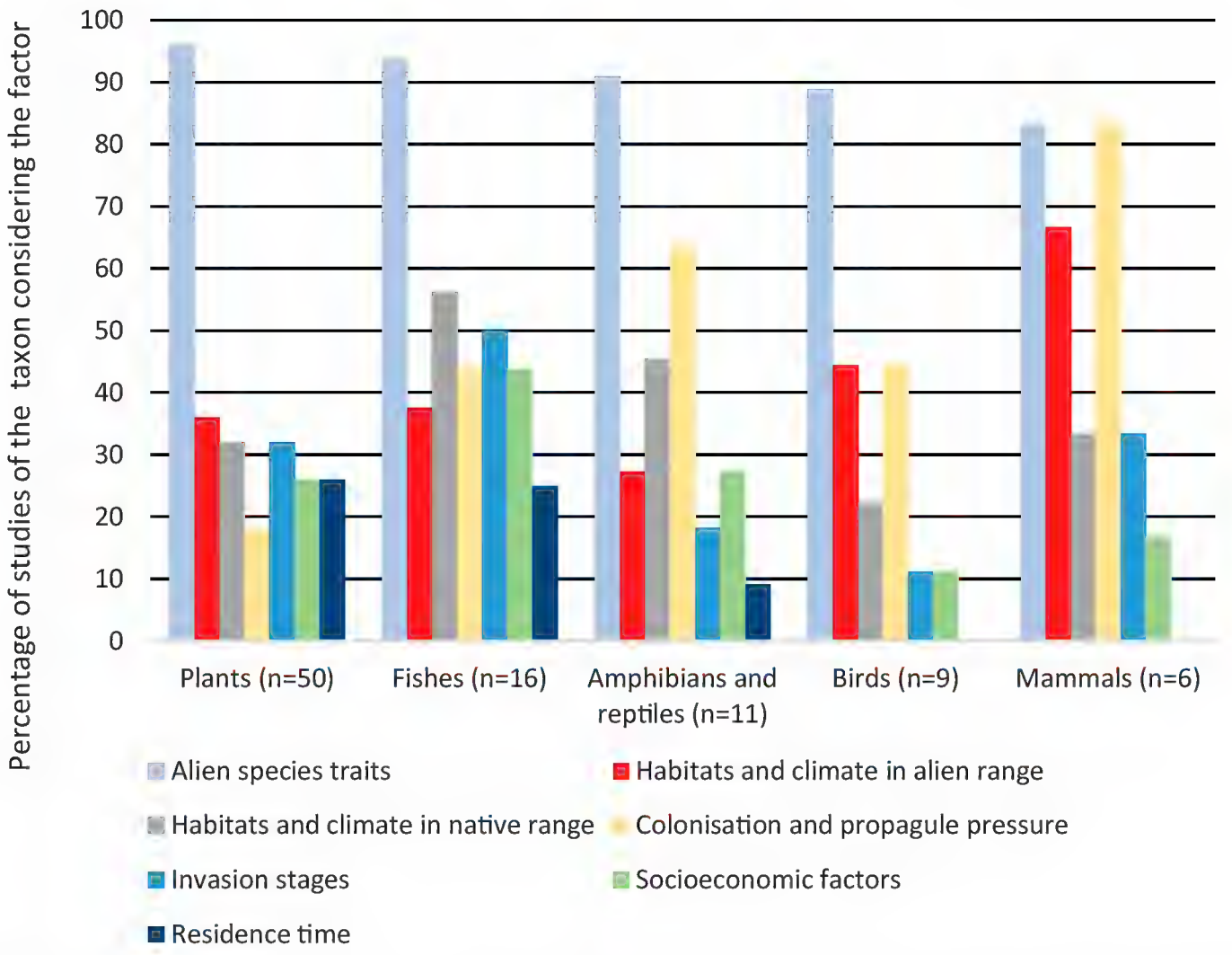

Figure 4. Overview of the frequency of factors included in 92 macroecological studies of plants and vertebrates. The figure shows that the majority of studies in all taxonomic groups focus on traits, but that there is a difference among plants and animals in the frequency of studies addressing propagule and colonisation pressure, that is greater in the latter. On the contrary, plant studies more commonly address the role of residence time. Based on studies listed in Appendix I ; note that studies on invertebrates, fungi, and cross-taxonomic studies are not shown here (n = 10).

ous quantitative surrogates have been used to attempt to capture variation in these key parameters. For example, the number of visitors to nature reserves (Lonsdale 1999; McKinney 2002), human population size or density (McKinney 2001, 2002; Pyšek et al. 2002; Taylor and Irwin 2004), the amount of trade and economic activity (Taylor and Irwin 2004; Pyšek et al. 2010; Essl et al. 2011a), species availability on the market (Dehnen-Schmutz et al. 2007a, b), the number of cultivars developed (Canavan et al. 2017), the type of land use such as the proportion of agricultural land and pastures (Chytrý et al. 2008b), or the number and distribution of botanic gardens (Hanspach et al. 2008; Hulme 2011) have all been used as proxies for propagule pressure in plants.

Despite the difficulty in accounting accurately for propagule pressure, it has been convincingly demonstrated that this factor, both over space (by widespread dissemination, abundant plantings, extensive release) and time (by long history of cultivation or captivity) fundamentally influences the probability of invasions by alien plant species (Rouget and Richardson 2003; Chytrý et al. 2008b). Models incorporating propagule pressure typically prove superior to those invoking only environmental parameters for

explaining distribution patterns and abundance of invaders at a regional scale (Rouget and Richardson 2003) and only once propagule pressure of invaders is factored out, can the real effects of diverse physical and biotic factors on the outcome of plant invasions be identified (Chaneton et al. 2002).

Naturalisation and invasion stage: establishment and spread [Traits & Location]

Anthropogenic factors in the transport and introduction stages of the invasion influence the identities and numbers of species available for establishment at different locations, and the composition of the founding populations of those species (event-related effects). In general, propagule pressure needs to be sufficiently high to allow the founding population to escape the stochastic effects of demography, environment, genetics, and Allee effects, although the inherently random nature of these effects means that some very small founding populations avoid them. Following introduction, features of the new environment (including resource availability, disturbance regimes, environmental conditions, and native biota), and the ways that these features interact with the biological traits of the alien species, come into play in determining which species establish viable and persistent populations. Effectively, these features and traits determine lineage survival probability (Fig. 2). Populations that establish can then go on to spread across the new environment, by an ongoing sequence of establishment events realised through (and depending on) both their life history traits and further human-mediated dispersal. The spatial and temporal patterns in the distribution, abundance, richness and traits of the alien species that result, and the relationships between these population- and community ecology processes, are the fodder of the macroecological patterns and large-scale biological invasions (Fig. 2).

Even at this 'terminal' point in the macroecological study of biological invasions, however, it is important to remember that observed relationships bear the imprint of previous stages in the invasion process (Leung et al. 2012; Donaldson et al. 2014). For example, the right-hand ('Invasion') part in Fig. 2 presents a cartoon of the distributional extent and abundance of four hypothetical established alien species, plus the relative spatial positions of those populations in an oval region. A naïve assessment of these patterns might conclude that species represented by the triangle and star are naturally more invasive, being more abundant and having wider distributional (and latitudinal, if we assume the figure maps to the cardinal points) extents than the species represented by the cross and crescent. Species richness appears to decrease from the top (north) to the bottom (south) of the region. Species in the north tend to have pointed edges, with that in the south having more curves (although sample size is low to make inferences about traits). However, all these conclusions need to be tempered by information on which species were introduced, where and when, and in what numbers. In Fig. 2, we see that more species were introduced to the north than the south; we see that introduced species in the south were more likely to have had curved edges, while those in the north were more likely to have had points. Those species that established were generally

those introduced in larger numbers. The star and triangle species were introduced more widely than the cross and crescent. The crescent species was only introduced in the south. All of this context modifies our conclusions, and demonstrates that we cannot reliably make the conclusions if we analysed only the current distribution pattern.

Field data for assemblages of alien species show that the effects depicted in Fig. 2 are real and complex. For example, the extent of the distribution ranges of established alien bird species increases with latitude poleward of the tropics, consistent with the well-known ecological pattern known as Rapoport's rule, but ranges are smaller in the tropics (Stevens 1989). However, this pattern is largely a consequence of the latitudinal distributions of where bird species have been introduced, which is only modified slightly by latitudinal variation in establishment (Dyer et al. 2020). Hence, while alien and native bird species both follow Rapoport's rule, the mechanisms underlying the similar patterns are unlikely to be the same (Dyer et al. 2020). The same is true for Bergmann's rule in alien and native bird species (Blackburn et al. 2019), as noted earlier.

Various elements of introduction context may also interact. For example, individual pathways can deliver species with different levels of invasiveness (Thellung 1912; Pyšek et al. 2011), and species arriving via different pathways may differ in the impacts they cause (Pergl et al. 2017). The way in which species are introduced and spread around by humans within the new range can also have long-lasting impacts on invasion patterns. For example, trees used for forestry tend to be introduced to a few rural sites in large numbers, whereas ornamental trees tend to be introduced to many urban sites in low numbers, leading to profound differences in the pattern of the occurrence of invasions across spatial scales (Donaldson et al. 2014).

Residence time [Event]

An important human-related effect on macroecological patterns of alien species that manifests most strongly in the naturalisation and invasion stages is residence time (Rejmánek 2000; Castro et al. 2005, Pyšek and Jarošík 2005, Williamson et al. 2009, Pyšek et al. 2011). For plants, residence time relates to species' geographic alien range sizes but also their invasion status – in the Czech Republic casual species have significantly shorter mean residence times than naturalised and invasive aliens (Pyšek and Jarošík 2005), and in south-east Australia, alien graminoids with longer minimum residence times are more likely to be classified as invasive than non-invasive (Catford et al. 2016). Many regions contain species that have not been present long enough for them to naturalise and become invasive – yet, the importance of any particular plant trait in determining the success or failure of invasion is discernible only after the species has either established or failed in a new region. The longer a species is present, the more it is provided with opportunities for adaptation and spread, i.e. the more windows of opportunity it will encounter (Johnstone 1986). Another example of interaction with residence time is the lack of natural enemies in the new region following introduction, such as pathogens, herbivores or parasites. This process can operate on the scale of

centuries, as shown for the accumulation of pathogens by alien plant species in North America (Mitchell et al. 2010).

Residence time interacts also with propagule pressure: the longer the species is present in a region, the greater the size of the propagule bank, and the greater the probability of dispersal, establishment, and founding of new populations (Rejmánek et al. 2005; Richardson and Pyšek 2006). In Europe, the effect of residence time is very long-term, and is still obvious after several millennia of plant invasions, as demonstrated for archaeophytes in the Czech Republic and UK (species introduced since the beginning of Neolithic agriculture until the end of Medieval; Pyšek et al. 2004a). Those archaeophytes that invaded soon after the beginning of Neolithic agriculture are still more common and have wider distribution ranges than those that arrived later (Pyšek and Jarošík 2005). Likewise, alien birds with longer residence times have larger alien range sizes worldwide (Dyer et al. 2016). However, the effect in birds is largely a consequence of species with longer residence times having been introduced to more locations, and only the effect of number of locations is significant in multivariate analysis (Dyer et al. 2016). Positive relationships between residence time and distributional extent have also been documented for many regional alien floras (Forcella and Harvey 1983; Crawley et al. 1996; Wilson et al. 2007; La Sorte and Pyšek 2009; see Rejmánek et al. 2005 and Pyšek and Jarošík 2005 for a review), although the influence of colonisation and propagule pressures here remain unexplored. Thus, failure to incorporate information on residence time may lead to spurious conclusions as, for example, we would expect species with different residence times to have different alien range sizes by chance alone (Wilson et al. 2007; Pyšek et al. 2009b, 2015).

Alien species traits [Traits]

To date, most invasion studies have attempted to explain the macroecological determinants of invasion by alien species and their assemblages by focusing on factors related to species traits and environmental characteristics, thus the interaction 'Species biological traits × Geographic attributes × Habitats × Climate'. Few studies have explicitly considered event-related factors and their interactions with other factors. Searching for traits associated with invasiveness is partly practically motivated, and there is growing evidence that some species are inherently better equipped, i.e. have a more suitable suite of traits, to become invasive after translocation to new areas by humans (Pyšek and Richardson 2007; van Kleunen et al. 2010b). Identifying species with the potential to become weedy or pests based on their traits should provide information on the likely mechanisms by which a species becomes invasive, and the likely impacts it will have. It therefore provides a template for assessing the likely success of management options (Novoa et al. 2020). To achieve this, however, we need to identify the "real" and direct effects of the respective traits that can be then included into risk-assessment schemes, because often traits are associated with biases (e.g. resulting from variation in propagule pressure, residence time, pathways, habitats or other factors that are not

explicitly addressed in analyses). Indeed, the few available studies that do account for this complexity suggest that the role of species traits is strongly context dependent, and that traits interact with other factors – there is a complex interplay of species' traits, habitats occupied in both the native and invaded range (Hejda et al. 2009, 2015), characteristics of recipient ecosystems and native communities (Catford et al. 2019), and human activities (which influence propagule pressure and residence time in the new region) in determining invasion in novel environments (Bacon et al. 2014). Using multivariate approaches to examine suites of species traits linked with invasiveness may help to account for some of this context dependence (Kimmel et al. 2019).

Recent research on alien plants has shown that some of the species traits that were not commonly considered in the past due to the lack of information for large numbers of species forming floras play important roles in invasions. Such traits include seed bank persistence (Gioria et al. 2019), germination characteristics (Brändle et al. 2003; Gioria and Pyšek 2017), reproductive traits such as fecundity (Moravcová et al. 2010, 2015), and karyological characteristics such as genome size and ploidy levels (Kubešová et al. 2010; Pandit et al. 2014). The results of our models are only as good as the information available, and not considering a key trait can result in the influence of another trait being spuriously over-emphasised. Similarly, it has been shown in birds that missing important factors in the analyses might identify spurious effects determining invasion success. For example, propagule pressure is a major driver of establishment success and has been shown to be correlated to many species' traits in alien birds, like native range or body size (Cassey et al. 2004c). Analyses ignoring propagule pressure misidentified such species' traits as drivers of invasion success (Blackburn and Duncan 2001b).

In a study of European plants naturalised in North America, the effects of species traits on invasion were indirect, via their effect on the number of native-range habitats occupied and frequency of cultivation in the native range, and the importance of the biological traits was nearly an order of magnitude less than that of the breadth of the habitat niche, propagule pressure, and residence time (Fig. 5; Pyšek et al. 2015). This agrees with a previous study that reported direct effects of biological traits on the global invasion of Central-European species only during the most advanced stage of invasive spread, while the effects of traits on the probability of a species becoming naturalised were indirect (Pyšek et al. 2009a). Both these plant studies used the source-area approach (Pyšek et al. 2004b), looking at the pool of native European species invading elsewhere, therefore ignoring potential selection effects and post-invasive evolution in traits (Guo et al. 2018), but this approach is justified by the fact that a large fraction of species do not need to undergo evolutionary change for invasion (Parker et al. 2013; Colautti et al. 2014) and behave the same way abroad as at home (Firn et al. 2011; Petitpierre et al. 2012).

Moreover, the traits that confer an advantage at one stage of the process and in a particular habitat may be neutral or even detrimental at another phase and/or in a different habitat. For example, while small genome size played a role in the naturalisation of alien species in the Czech Republic, it did not separate invasive species from those that are not invasive (Kubešová et al. 2010; see also Küster et al. 2008).

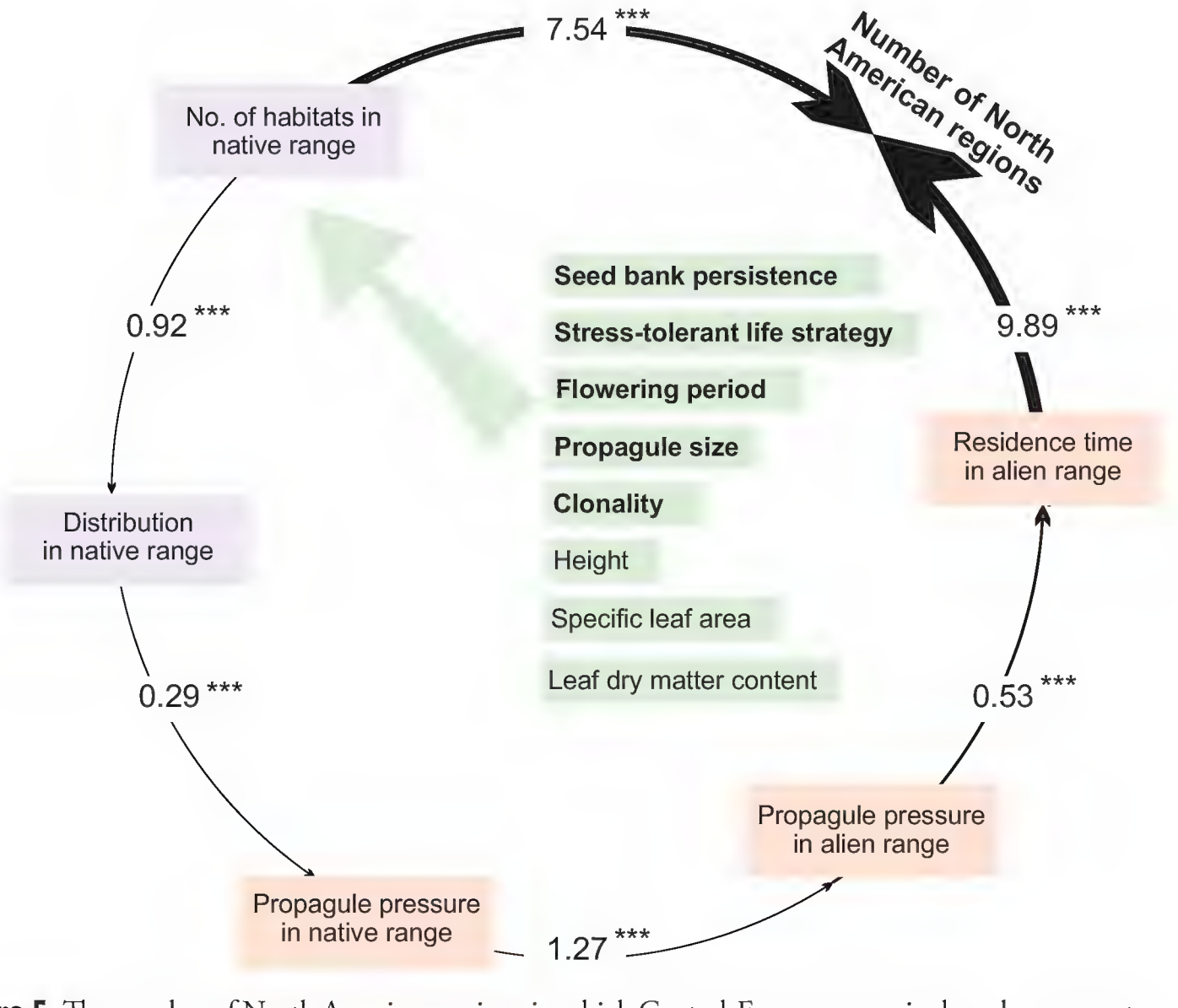

Figure 5. The number of North American regions in which Central-European species have become naturalised is driven by the combination of factors related to geographic attributes (the species' performance in its native range, i.e. habitat niche and distribution); propagule pressure (measured by using proxies related to human use of the species both in its native and invaded range) and residence time (the time since introduction to North America) that represent the event-related factors; and a suite of alien species traits that affect the species' invasion success indirectly, via their effect on the habitat niche in the native range (see Fig. 1 and 2 for explanation of colour codings); significant traits are shown in bold. The width and magnitude of numbers on arrows showing relationships between drivers is proportional to the value of the coefficient. Significance is indicated as: *** $p < 0.001$. Adapted from Pyšek et al. 2015.

Habitats [Location]

To know whether a region, community or habitat is more invasible we need to ask not only whether it has more alien species, but whether it is intrinsically more susceptible to invasions. Intrinsic invasibility can only be determined if processes of immigration and extinction are taken into account (including colonisation pressure), as pointed out by Lonsdale (1999), and if the relative invasiveness of the pool of invading species is also considered (Catford et al. 2012). Lonsdale's concept of invasibility has proved extremely useful in emphasising the role of colonisation pressure (although he used the term 'propagule pressure') and pointing out the difference between invasibility

(or vulnerability to invasion) of a region, community or habitat and a simple number of invasive species it harbours; for the latter the term 'level of invasion' has become broadly used (Chytrý et al. 2005; Hierro et al. 2005; Catford et al. 2012).

There is a consensus in the research community that in biological invasions, the invaded habitats and invading species are 'a key-lock principle', and need to be studied in concert for a complete picture (Shea and Chesson 2002). The majority of hypotheses in invasion ecology have received support in some circumstances (and failed in others), but those hypotheses that merge the habitat- and species-perspective perform best (Richardson and Pyšek 2006; Jeschke et al. 2012). At the regional scale of temperate Europe, the type of habitat that is invaded by alien plants has been shown to play an even greater role than climate and propagule pressure (Chytrý et al. 2008b). Yet, studies exploring factors underlying the outcome of species introductions at the regional and global scale, even those that do include a number of different factors, usually do not consider the identity and characteristics of habitats (e.g. structure, disturbances regimes, nutrient or water supply, etc.), in either native nor alien distribution range (Appendix I). This is of key importance because these habitat characteristics determine the mechanisms of invasion acting in a particular site; yet, papers that to some extent combine the effect of habitats with other factors are exceptions rather than the rule (Pyšek et al. 2015).

Available analyses comparing the range of habitats occupied by species in their native and invaded range suggest that for some species there is a shift in habitat use attributable to the invasion process. While naturalised plant species inhabit a comparable spectrum of habitats in both ranges, invasive species tend to occupy a wider range of habitats in their invaded than in their native range (Hejda et al. 2009). This supports the idea that the invasion phase of the process is associated with extension of the spectrum of occupied habitats, hence broadening species' habitat niches (Pyšek et al. 2009a). Another research direction in habitat-oriented invasion ecology is looking at habitat affinities that alien species exhibit in their native range and analysing how this preadaptation affects their success as invaders (Hejda et al. 2015; Kalusová et al. 2017). In a study of European plants introduced to North America, the direct effect of native-range habitat legacy and residence time were the main factors associated with the likelihood that a species would naturalise – more important than propagule pressure measured by a proxy related to species' human use (Fig. 5; Pyšek et al. 2015). This key role of habitat legacy in shaping invasion dynamics accords with studies showing the strong effect of the breadth of habitat niche on invasion success (Hejda et al. 2009; Kalusová et al. 2013) and supports the notion that abundant, widely distributed species are superior competitors due to their ability, acquired over evolutionary history, to tolerate a wide range of abiotic conditions, use a broad spectrum of resources, and resist a large number of potential enemies (Sax and Brown 2000). Macroecological studies that explore how species with different traits interact with habitat characteristics are rare (but see Divíšek et al. 2018); more work on this topic is needed to improve our understanding of this kind of context dependence in invasion macroecology.

One of the main reasons why, in the majority of models of plant naturalisation and invasion, habitats are not considered is the lack of data on habitat affinities of alien species for most continents other than Europe (see Chytrý et al. 2016), and on the variation in this characteristic by regions. Since habitats have a strong effect on the outcome of invasion (Chytrý et al. 2008a, b) and on the way alien species integrate into local communities (Divíšek et al. 2018), such models may provide biased results or yield a low predictive ability due to exclusion of this important determinant. Similarly, testing of hypotheses in invasion ecology without taking habitats into account may mask the validity of concepts that do not hold across all environments, but may still be true under specific circumstances.

Another aspect of the interaction of habitat with pathway is that alien species intentionally brought into new regions (e.g. pets, aquarium related introductions, and horticulture) often escape or are released in places with suitable local conditions (e.g. similar habitats as in their native range) or close to human settlements and other sites favourable for alien species spread such as harbours, roads, etc. Given that the majority of successful alien plants are introduced through horticulture (Hanspach et al. 2008; Lambdon et al. 2008; Pyšek et al. 2012; van Kleunen et al. 2018), this phenomenon may have important consequences for macroecological patterns.

Recommendations: statistical and modelling considerations, and data gaps

Models aimed at predicting absolute alien species richness have a low to moderate accuracy in the region where they were developed and poor accuracy in new regions (Capinha et al. 2018). Predictions of relative species richness also suffer from limitations. We argue that such problems are largely attributable to the failure of the models to give adequate attention to the multitude of processes affecting invasion outcomes. We have proposed a comprehensive typology of factor classes and their interactions that are needed to explain invasions: alien species traits, location characteristics, and event-level factors (Fig. 1). These three classes of factors can be further subdivided, e.g. location-related factors into geography/topography, habitat, and climate (see above). All these factors, however, might interact differently at specific stages of the invasion process. These interactions must be given explicit consideration in macroecological analyses of invasive aliens to arrive at sensible conclusions. A framework for stage-specific best-practise risk-assessment (TEASI; Leung et al. 2012), which explicitly addresses Transport, Establishment, Abundance, Spread, and Impact, could be combined with approaches that recognise the context dependence at each stage. Related to this, one needs to be explicit about the response variable analysed, be it the likelihood of being introduced, overcoming the naturalisation threshold, or range size, spread rate, or impact. Many studies do not distinguish adequately among response variables and simply name them "invasion success" or similar.

Methodologically, a wide range of approaches is available, though many are not frequently employed. An increasing number of studies employ the source-area

approach (Prinzing et al. 2002; Pyšek et al. 2004b; Thuiller et al. 2005; van Kleunen et al. 2007; Blumenthal et al. 2009; Bucharova and van Kleunen 2009; Mitchell et al. 2010; Pyšek et al. 2015), where a source pool of species native to a certain region is followed for their post-introduction performance in another region. Focusing on this specific trajectory allows us to minimise confounding variation that arises when multiple source areas of introduction are considered, both in terms of evolutionary predispositions acquired in disparate regions of origin, as well as various historical contingencies that shape introduction dynamics. Using a source-pool approach, Pyšek et al. (2015) used species traits, habitats, propagule pressure, and residence time to model the number of regions in North America colonised by Central-European plant species. To do so, they employed confirmatory path analysis (structural equation modelling) on a complex invasion model. Few studies have analysed which species in a particular source pool have been translocated, the characteristics of those species or the reason for the introduction, with the exception of bird introductions (see above). However, this is a key omission, as observed differences may be entirely due to which species in the source area were selected for translocation. Once in the new region, target-region specific analyses (see van Kleunen et al. 2010a) are sensible, recognising, though, the properties of the specific species pool that arrived.

Using joint species distribution models, O'Reilly-Nugent et al. (2019) modelled changes in the cover of alien and native plant species, and were able to identify three out of 72 aliens that were having a strong competitive impact on the community. Though at a different scale, the method seems appropriate to be applied in the MAFIA framework. A range of methods for joint species distribution modelling, applicable across various scales, are now available (e.g. Pollock et al. 2014). Golivets et al. (2019) studied complex, non-linear relationships between environment and plant invasions into forests, using boosted regression trees and non-linear Bayesian regression.

With the development of Community Assembly by Trait Selection (CATS; Shipley et al 2006; Warton et al. 2015b) the classical fourth-corner problem (Legendre et al. 1997) and its implementation in joint models for abundance (Warton et al. 2015a), the analysis of trait × environment interactions, have become much more powerful and flexible. Milanović et al. (2020) used this method to relate environmental variables and traits with the area of occupancy in Germany with respect to different stages of the invasion process. In another stage-specific approach, Catford et al. (2019) used hierarchical linear regression models (Pollock et al. 2012; Jamil et al. 2013) to identify variables associated with invasion of non-resident species. Their indicators of invasion success were occupancy and abundance at two stages of invasion (establishment and spread).

We believe that the approaches outlined above will also be applicable to model further interactions, such as traits × temporal dynamics, or traits × propagule pressure. We are, though, unaware of an approach that incorporates interactions among all three classes of factors mentioned above (location, event, species) in a framework that considers the resulting species pool of a previous stage in the invasion process, as to derive unbiased conclusions throughout all stages. Most promising are complex hierarchical Bayesian approaches (see Zurell et al. 2016 for a dynamic species distribution modelling

approach) consisting of different submodules separately modelling each stage and providing the results to the next step in the analysis.

All the models above are only applicable if the data are of sufficient quality. Data gaps can constrain our understanding of invasion processes. In particular, we often know little about key anthropogenic factors – notably colonisation pressure and propagule pressure. These factors must be considered to obtain an unbiased view of the processes, but there are few reliable proxies for such factors (Blackburn et al. 2020). Similarly, analyses can be biased if data on key species traits are missing (e.g. because they are logistically difficult to collect, such as reproductive traits of plants; Moravcová et al. 2015). Therefore, data should be collected in a comparative manner, rather than taken from opportunistic observational data. Such ad hoc data will be biased by habitat, native vs invaded region (Parker et al. 2013), and other contexts, and hence frequently show larger within-species variation than among-species variation (see Kattge et al. 2020). For example, fecundity expressed as the amount of seeds produced, based on data collected in a comparative manner, was one of the most important traits discriminating naturalised and invasive species in the Czech flora (Moravcová et al. 2010, 2015). More detailed information on seed bank longevity beyond the simple categorisation based on whether a species builds a persistent seed bank (Kleyer et al. 2008), such as the amount, density, and survival times of seeds in the soil is also still largely not available, yet this trait has been recently shown to be of importance for naturalisation and invasion (Gioria et al. 2012, 2014). Similarly, increasing knowledge on dates of introduction of alien species to particular regions of the world and accumulation of such data in the First Records Database has improved our understanding of temporal dynamics of biological invasions at the global scale (Seebens et al. 2017, 2018). For the detection of alien species, remote sensing techniques represent a promising tool for obtaining information across large scales on some components of MAFIA such as habitat structure, resource availability, land-use, as well as proxies for propagule pressure (e.g. Weiers et al. 2004; Huang and Asner 2009; Skowronek et al. 2017; Vaz et al. 2019). To date, remote sensing has largely been used to detect the spatial distribution of alien species in space and time, and its use to derive explanatory macroecological variables to interpret such patterns has so far been limited.

To some degree, incomplete data on invasions might be comparable to incomplete citizen science species distribution data. These suffer typically from heterogeneous and non-random sampling, false absences, false detections, and spatial autocorrelation in the data. To overcome these problems, occupancy models are increasingly used (Altwegg and Nichols 2019). They consist of two different elements, separating the observation process from biological processes. In invasion ecology, a module accounting for observational bias might be a solution. In the context of the MAFIA, it would be useful to explore whether a similar approach could be used, i.e. incorporating a model component accounting for imperfect detection or knowledge of introduction processes, but the field of model-based data integration is quite new and evolving (Isaac et al. 2020). Simple models, i.e. those just adding additional proxies as covariates, are likely to be inappropriate to account for the biases in knowledge and detection. In non-

manipulative observational studies in particular, one needs critically to discuss whether their data are appropriate to derive the conclusions drawn and which biases in input data are likely to cause certain biases in results.

Our understanding of the role of macroecological processes in invasions can only advance if we are able to build a mechanistic framework that incorporates the most relevant factors (event, location, species) and their interactions, as well as biases that arise through human selectivity along the invasion sequence, resulting from the fact that invasions are part of a 'coupled human and natural system' (Sinclair et al. 2020, see also Howard 2019). We believe that the MAFIA is helpful for conceptualising these issues, by explicitly identifying the pathway along which alien macroecological patterns develop, and how biases in observed patterns may be inserted by this pathway. This will hopefully help a mechanistic understanding to emerge. It may also help us to think critically about how we collect and analyse data, striving to measure the relevant factors in a meaningful way instead of indiscriminately adding proxies to oversimplified models. Only if we manage to combine both will invasion ecology become a more predictive discipline.

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Appendix I

Overview of 102 macroecological studies on biological invasions and their classification according to the factors included in the analysis (indicated as ×). The studies were found and selected from 5 literature searches done in Google Scholar using the following terms: (1) predict AND "invasive species", (2) success AND "invasive species" AND "amphibians", (3) success AND "invasive species" AND "birds", (4) success AND "invasive species" AND "mammals", (5) success AND "invasive species" AND "plants", and (6) success AND "invasive species" AND "reptiles". The results of the searches were sorted using the default option "by relevance". From search 1 we reviewed the first 500 results, while we reviewed the first 100 results from searches 2–6. The information on studied organism, scale and main conclusions of each study is provided. The overview does not aim at being exhaustive and includes studies on plants (50), fishes (16), amphibians and reptiles (11), birds (9), mammals (6), vertebrates in general (2), amphipods (1), ants (1), aquatic species (1), arthropods (1), fungi (1), macroinvertebrates (1), wasps (1), and one general study. Note that we do not indicate whether the data on alien species traits come from the native or alien range because in many studies it was difficult to infer where they were measured. The colour coding correspond to that used in Figs 1, 2. IAS = invasive alien species.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Alcaraz et al. 2005	Fishes	Native and IAS in the Iberian Peninsula	×	×	×	×				IAS generally have larger latitudinal ranges than natives.
Allen et al. 2013	Vertebrates	Alien species in peninsular Florida	×	×	×		×		×	Predictors of establishment and spread differ across vertebrate taxa.
Allen et al. 2017	Amphibians and reptile	Global	×				×		×	Fast life history traits promote invasion success in amphibians and reptiles.
Amiel et al. 2011	Amphibian and reptiles	Global	×				×		×	Introduced alien species with larger brain sizes are more likely to establish and invade.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Andersen 1995	Plants	Alien species in Denmark	×		×					Alien species, especially in seminatural habitats, are more likely than natives to present fleshy fruits and be dispersed by wind.
Aronson et al. 2007	Woody plants	Alien species in New York	×							Fruit type, life form and origin influence establishment success.
Bacon et al. 2014	Arthropods	Europe		×	×	×	×		×	Quarantine arthropods are more likely to establish if climate matches and hosts are available; propagule pressure only plays a role if these conditions are met.
Ben Rais Lasram et al. 2008	Fishes	Lessepsian fish species invading the Mediterranean Sea	×	×	×	×		×		Residence time and climate match between the native and alien ranges influence invasiveness.
Blackburn et al. 2009	Birds	Global	×						×	Alien species are less likely to be introduced when presenting traits that predispose them to Allee effects. Alien species that can cope with novel environments and have larger body mass have a higher establishment success.
Blackburn and Duncan 2001a	Birds	Global	×	×	×					Avian introduction success depends on the suitability of the abiotic environment at the introduction site.
Blackburn and Duncan 2001b	Birds	Global	×	×	×					The establishment success of exotic birds depends on introduction efforts.
Bomford et al. 2009a	Mammals	Alien species introduced to New Zealand, Australia and Britain		×	×		×			The number of release events and the climate-match between the native and introduced ranges influence establishment success.
Bomford et al. 2009b	Reptiles and amphibians	Global		×	×		×			Introduction effort, climate match and invasiveness elsewhere facilitate the establishment of introduced species.
Bucharova and van Kleunen 2009	Woody plants	North American species introduced into European garden and parks	×			×	×	×		Planting frequency determines naturalisation success.
Cadotte and Lovett-Doust 2001	Plants	Alien species in Canada	×							Alien species are more likely than natives to be annual and biennial, hermaphrodite, have long flowering periods and small fruits, and are less likely to be dispersed by animals. In seminatural habitats, aliens are also more likely to be trees with a high number of seeds per fruit.
Cadotte et al. 2006	Plants	Alien species in Canada	×	×	×					Abundant aliens are more likely to have longer flowering duration, be native to Europe or Eurasia, and grow in variable soil moisture conditions.
Cadotte et al. 2009	Plants	Alien species in Royal National Park (Australia) and the whole Australia	×		×					Relatedness with other IAS can be a useful predictor of invasion success at large spatial scales but not at smaller, landscape scale.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Capellini et al. 2015	Mammals	Global	×				×		×	Introduced mammals are likely to be highly productive and have a high reproductive output. Greater reproductive output and introduction effort increases success at both the establishment and spread stages.
Cassey et al. 2005	Birds	Global	×		×		×			The characteristics of the introduction events are the most consistent predictors of establishment success.
Colautti 2005	Salmonoid species (fishes)	Alien species in Nevada, USA	×	×	×		×		×	Species presenting large sizes, weight and latitudinal ranges are more likely to be introduced. Propagule pressure affects establishment.
Crawley et al. 1996	Plants	Alien species in the British Isles	×							Aliens are likely to be taller, present larger seeds and no or protracted dormancy, flower earlier or later, and present more pronounced r- or K-strategies than natives.
Dawson et al. 2009	Plants	Alien species introduced to Amani Botanical Garden, Tanzania	×	×			×	×	×	Residence time, growth rate, number of seeds per fruit, seed mass, dispersion by canopy-feeding animals and tolerance to shade facilitates naturalisation.
Dehnen-Schmutz et al. 2007a	Plants	Ornamental plants introduced to Britain				×	×			The period of time a species is available in the market, the number of nurseries selling it and the price of its seeds influence invasion success.
Devin and Beisel 2007	Gammarid amphipods	Alien species native to Western Europe and North America	×	×						Tolerance to salinity increases invasiveness. Invasiveness is affected by a combination of several traits.
Divíšek et al. 2018	Plants	Alien species in temperate Central Europe	×		×				×	Similarity to native species facilitates naturalisation, while dissimilarity facilitates invasions.
Drake 2007	Fishes	Global	×							Parental investment and fecundity influence establishment success.
Duggan et al. 2006	Freshwater fishes	Alien species introduced to Canada and USA	×				×		×	Propagule pressure and body size affect introduction and establishment.
Duncan 1997	Passeriform birds	Alien species introduced to New Zealand					×			Introduction effort (i.e. number of introductions and number of introduced individuals) could predict the invasion success of passeriform birds.
Ellstrand and Schierenbeck 2006	Plants	Global	×							Hybridization stimulates invasiveness.
Ferreira et al. 2012b	Amphibians and reptiles	Global	×							Amphibians and reptiles have similar establishment success.
Ferreira et al. 2012a	Reptiles	Global	×							The presence and richness of native congeners increase establishment success.
Forsyth et al. 2004	Mammals	Alien species introduced to Australia	×		×		×		×	Climate suitability, alien range size, and introduction effort increase establishment and spread.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Fujisaki et al. 2010	Reptiles	Alien species in Florida	×	×			×			Taxonomic order, maximum temperature match between native range and Florida, sale price, and manageability (difficulty to manage the species as a pet) are significant predictors of establishment success.
Gallagher et al. 2011	*Acacia* sp. (plants)	Alien species native to Australia	×	×						IAS are more likely than non-invasive aliens to be shrubs or trees and have large native ranges.
Gallagher et al. 2015	Plants	IAS in Australia	×	×				×	×	IAS are more likely than naturalised species to be tall and have large specific leaf area, long flowering periods, and high tolerance to environmental conditions in their native range .
García-Díaz and Cassey 2014	Amphibians	Alien species in Australia	×	×		×	×			The availability to be captured, bred and housed in captivity increases the probability of amphibians to be introduced to and transported within Australia.
Gassó et al. 2009	Plants	IAS in Spain	×	×	×	×		×		Wind dispersal, minimum residence time, anthropogenic disturbance, low altitude, short distance to the coastline and dry and hot weather conditions increase invasiveness.
Godoy et al. 2011	Plants	Native and alien species in the Mediterranean region	×							IAS are more likely than native species to present high capacity for carbon gain and high performance over a range of limiting to saturating resource availabilities. Invasive and native species do not differ in their phenotypic plasticity.
González-Suárez	Mammals	Global	×				×			Intraspecific variation in morphological traits increases establishment success.
Goodwin et al. 1999	Plants	European species invading Canada	×							IAS are more likely than non-invasive aliens to be tall and have long flower-periods.
Grabowska and Przybylski 2015	Freshwater fishes	Alien species invading Central Europe	×							Life history traits facilitate the invasion of freshwater fishes in Central Europe.
Gravuer et al. 2008	*Trifolium* sp. (plants)	Species invading New Zealand	×	×		×	×	×	×	Success at all invasion stages is more influenced by biogeographic factors than biological attributes. Biological traits only influence the selection of species for introduction and the relative rates of spread. Different factors determine the probability of plant introduction, naturalisation, and spread.
Grotkopp et al. 2010	Woody horticultural plants	Global	×							IAS have higher relative growth rates than non-invasive aliens.
Hamilton et al. 2005	Plants	Alien species in Eastern Australia	×		×			×		Seed size affects invasion success at both regional and continental scale, while SLA only affects invasion success at continental scale.
Herron et al. 2007	Trees, shrubs and vines (plants)	Species invading New England (USA)	×						×	IAS are likely to have previous invasion history, large native latitudinal ranges, rapid growth rates and non-evergreen leaves. Invasive trees are likely to tolerate shade.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Higgins and Richardson 2014	*Acacia* sp. and *Eucalyptus* sp. (plants)	Alien species native to Australia	×	×					×	IAS have larger potential range sizes than naturalised aliens. Naturalised aliens have larger potential range sizes than non-naturalised aliens. The effect of traits on invasion success is context dependent.
Jansen et al. 2011	Plants	Alien species in north-eastern Germany			×					Different alien species have different ecological preferences.
Jeschke and Strayer 2006	Vertebrates	Species native to Europe or North America	×				×		×	Propagule pressure and human affiliation affect invasion success across taxa and invasion stages. All other factors affect invasion success differently, specially depending on the invasion stage.
Kolar and Lodge 2002	Fishes	Species alien to the Great Lakes	×			×			×	Aliens are more likely to establish if they present fast growth, tolerate wide temperature and salinity ranges and have a history of invasiveness elsewhere. Aliens with slow growth and tolerating wide temperature ranges spread fast. Nuisance aliens were more likely to have smaller eggs and wider salinity tolerances than non-nuisance aliens.
Küster et al. 2008	Plants	Species invading Germany	×							Among IAS, different ecological strategies (determined by particular combinations of traits) facilitate invasion.
Lake and Leishman 2004	Plants	Alien species in Sydney, Australia	×	×					×	IAS have higher specific leaf area and are more likely to disperse by wind and vertebrates, and less by ants, than non-invasive aliens or natives. In disturbed sites, IAS have smaller seeds and flower longer than natives. Aliens have softer leaves and are more likely to propagate vegetatively than natives.
Lester 2005	Ants	Alien species in New Zealand	×		×		×			Mean temperature at the highest latitude of the introduced range and interception rate determine establishment success.
Lloret et al. 2005	Plants	Alien species in Mediterranean islands	×		×					Aliens are more likely to be more abundant if they reproduce vegetatively, have large leaves, flower in summer for long periods of time and are dispersed by wind and animals. Aliens are more likely to have succulent and fleshy fruits in ruderal and seminatural habitats, respectively.
Lockwood 1999	Birds	Global	×			×				Taxonomy influences the transport and establishment of alien birds.
Maitner et al. 2012	Birds	Introduced species in Florida, New Zealand, and Hawaii	×							Close relatedness to the extant avifauna increases establishment success.
Marchetti et al. 2004a	Fishes	Alien species in watersheds in California, USA	×	×			×		×	Aliens' traits (trophic status, size of native range, parental care, maximum adult size, physiological tolerance, distance from nearest native source) and propagule pressure influence establishment. Physiological tolerance and propagule pressure predict spread. Previous invasion success predicts species integration and impact.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Marchetti et al. 2004b	Fishes	Aliens in catchments in California, USA	×				×		×	Parental care, physiological tolerance, propagule pressure and previous invasion success predict alien species establishment. Life span, distance from nearest native source, trophic status and prior invasion success predict spread. Maximum size, physiological tolerance and distance from nearest native source predict abundance.
McGregor et al. 2012	*Pinus* sp. (plants)	Alien species introduced to Great Britain and New Zealand	×	×	×		×	×		Human factors are better predictors of introduction and naturalisation than species or biogeographic traits.
Milbau and Stout 2008	Plants	Alien species in seminatural habitats in Ireland	×	×	×	×		×	×	Clonal growth, moisture-indicator value, nitrogen-indicator value, native range, and date of first record affect naturalisation. Ornamental introduction, hermaphrodite flowers, pollination mode, being invasive elsewhere, onset of flowering season, moisture-indicator value, native range, and date of first record affect invasiveness.
Møller et al. 2015	Birds	Alien species introduced in oceanic islands	×		×		×			The ability to thrive in urban areas facilitates the establishment and invasion of birds in oceanic islands.
Moodley et al. 2013	Proteaceae (plants)	Global	×						×	Naturalised aliens are more likely than non-naturalised aliens to have large native ranges, low susceptibility to Phytophthora root-rot fungus, large mammal-dispersed seeds, and the capacity to resprout. IAS are more likely than naturalised species to have large native ranges, be used as barrier plants, be tall and serotinous and have small seeds.
Moravcová et al. 2010	Plants	Alien species in the Czech Republic	×						×	IAS are more likely than naturalised aliens to have a low length/width ratio of propagules, fewer seedlings establish in the autumn, have better capacity for dispersal by wind, and be more fecund.
Moravcová et al. 2015	Herbaceous plants	Alien species in the Czech Republic	×						×	Seed production, propagule properties and height affect invasiveness at the reproduction, dispersal and competition stages respectively.
Moyle and Marchetti 2006	Freshwater fishes	Alien species in California, USA	×	×	×	×	×		×	Different traits affect different stages of the invasion process.
Novoa et al. 2015	Cactaceae (plants)	Global	×			×				Growth form and native range size influence invasiveness.
Olden et al. 2006	Freshwater fishes	Native and alien species in the Colorado River Basin, USA	×	×						Alien opportunists have the highest rates of spread.
Ordonez et al. 2010	Plants	Global	×							Functional trait differences between alien and native species contribute to the success of alien species.
Paavola et al. 2005	Aquatic species	Alien species in European brackish water seas	×		×					Alien species are adapted to the salinity levels of areas with the lowest richness of native species.
Pemberton and Liu 2009	Ornamental plants	Alien species in Florida, USA	×	×			×	×		Propagule pressure and residence time increase the probability of naturalisation. Naturalised aliens are likely to have large native range sizes, be aquatic herbs or vines and belong to the families Araceae, Apocynaceae, Convolvulaceae, Moraceae, Oleaceae or Verbenaceae.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Philibert et al. 2011	Forest pathogenic fungi	Alien species in Europe	×	×				×	×	Long-distance dispersal, sexual reproduction (in addition to asexual reproduction), spore shape and size, number of cells in spores, optimal temperature for growth and parasitic specialization (host range and infected organs) determine invasiveness.
Prinzing et al. 2002	Plants	European species invading Argentina	×		×	×				IAS are likely to have r-strategy; prefer warm, dry, sunny and nitrogen-rich habitats; and to be used by humans.
Pyšek et al. 1995	Plants	Species introduced to the Czech Republic	×		×	×				Aliens are more likely than natives to be C- and CR- strategists and dispersed by humans. They prefer dry, warm and nutrient-rich habitats. In semi-natural habitats, aliens are mainly tall hemicryptophytes escaped from cultivation. In human-made habitats aliens are mainly therophytes or geophytes, introduced spontaneously.
Pyšek 1997	Plants	Global	×		×	×			×	Clonal alien species are more likely than non-clonal aliens to be introduced deliberately. In wet, old and natural habitats, IAS are more likely than non-invasive aliens to be clonal. However, clonality has a negative effect on invasion success during the dispersal stage.
Pyšek and Jarošík 2005	Plants	Alien species in the Czech Republic	×	×		×	×			American and Asian aliens are likely to disperse by water. Life strategy, origin and dispersal mode are likely to affect invasion success. Residence time determines the influence of height and growth form on invasion success.
Pyšek et al. 2009a	Plants	Aliens native to Central Europe	×	×					×	The characteristics of the native habitats are likely to affect the early stages of invasion, while species traits are more likely to affect later stages.
Pyšek et al. 2009b	Woody plants	Aliens cultivated in the Czech Republic	×				×	×	×	Residence time in Czech Republic and Europe increases the probability of an alien species scaping from cultivation and naturalising respectively. Propagule pressure increases the probability of an alien species escaping cultivation. Species from Asia with small fruits are more likely to naturalise. Residence time and the ability of tolerating low temperatures increase invasiveness.
Pyšek et al. 2010	General	Naturalised species in Europe		×	×	×				National wealth and human population influence invasiveness.
Pyšek et al. 2011	Plants	Species introduced to the Czech Republic	×		×	×		×	×	Human assistance facilitates naturalisation and invasion.
Pyšek et al. 2015	Plants	European aliens naturalising in USA	×	×			×	×		Residence time and number of habitats occupied in the native range are likely to affect the number of occupied regions in the non-native range, while species traits have an indirect effect on naturalisation success.
Ribeiro et al. 2008	Freshwater fishes	Aliens in watersheds in the Iberian Peninsula	×	×			×		×	Prior invasion success affects all the stages of the invasion process. The traits that affect invasiveness are context dependent.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Rossinelli and Bacher 2015	Parasitic wasps	Global	×	×	×	×	×		×	Parasitic wasps with a narrow host range introduced for biocontrol establish better.
Ruesink 2003	Freshwater fishes	Global	×	×	×	×		×		Aliens that are intentionally introduced several times to a particular area are likely to have impacts.
Ruesink 2005	Freshwater fishes	Global	×	×	×	×	×	×		Aliens are more likely to establish when having small body size, high reproduction rates, are generalists and omnivores, are introduced to isolated areas with high endemism of fish fauna and humans support their establishment.
Sol et al. 2008	Mammals	Global	×	×	×	×	×			Alien mammals with large brains relative to their body mass establish better.
Sol et al. 2012	Birds	Global	×				×			Successful invaders are characterised by life-history strategies in which they give priority to future rather than current reproduction.
Statzner et al. 2008	Macroinvertebrates	Alien species in natural European stream sites	×							IAS are more likely than natives to reproduce frequently; have higher propagule pressure, more ovoviviparity, larger size and longer life; exploit food resources more effectively; and tend to be more dominant in their communities and survive during dispersal.
Sutherland 2004	Plants	Alien species in the USA	×						×	Aliens are less likely than natives to be clonal and adapted to wetlands. IAS are more likely than non-invasive aliens to be monoecious, self-incompatible, perennial and woody.
Thiébaut 2007	Aquatic and semi-aquatic plants	Species native to or invasive in North America and France	×							No differences were found in the distribution and biology of aquatic and semi-aquatic plants between their native and invasive ranges.
Thompson et al. 1995	Plants	Species expanding in England, Scotland, the Republic of Ireland and the Netherlands	×		×					Aliens are more likely than natives to be clonal and present transient seed banks.
Thuiller et al. 2006	Plants	Species invading South Africa	×	×	×	×		×		The distribution of IAS is best explained by the use of species by humans. Different sets of traits affect invasion success in different geographic areas.
Tingley et al. 2010	Amphibians	Global	×	×		×				Introduced species are more likely to be native to the Northern Hemisphere, have large ranges and be sympatric with high densities of humans than non-introduced species. Intentionally introduced species are of larger body size, occupy higher elevations in their native ranges, and are more likely to be native to the Northern Hemisphere than unintentionally introduced species.

Reference	Studied organism	Scale	Alien species traits	Habitats and climate in native range	Habitats and climate in alien range	Socioeconomic factors	Colonisation and propagule pressure	Residence time	Invasion stages	Conclusions of the study
Tingley et al. 2011	Amphibians	Global	×	×	×	×	×	×		The presence and richness of native congeners increase establishment success. Establishment success is higher on islands and in areas with abiotic conditions similar to the native range and with higher presence and richness of native congeners.
van Kleunen et al. 2007	Family Iridaceae (plants)	Species native to Southern Africa	×	×		×				Naturalised aliens are likely to come from low altitudes, have high numbers of subtaxa and be tall.
van Kleunen and Johnson 2007	Plants	European species invading the USA	×							IAS are likely to be self-compatible.
van Kleunen et al. 2010b	Plants	Global	×							IAS are more likely than non-invasive aliens to have high values for performance traits.
van Wilgen and Richardson 2011	Reptiles	Alien species introduced to California and Florida	×							Phylogenetic distance with native species increases establishment success.
van Wilgen and Richardson 2012	Reptiles and amphibians	Alien species introduced to California and Florida, USA	×		×		×			Alien species, especially lizards and frogs, which mature early and come from environments similar to that of the introduction region are likely to establish.
Vila-Gispert et al. 2005	Freshwater fishes	Native and IAS in Catalan streams, Spain	×					×		Aliens are more likely than natives to have large size, long longevity, late maturity, high fecundity, few spawnings per year, and short reproductive span. Species traits do not clearly differentiate native from alien species. Residence time increases invasion success.
Wonham et al. 2000	Fishes	Global				×			×	Different fish families differ in the frequency at which their species are transported and introduced through ballast water, and in their establishment success in the introduced areas.
Williamson and Fitter 1996	Plants	Alien species in Great Britain	×		×					IAS are more likely than natives to be tall, taller than wide, phanerophytes and insect-pollinated and to have large leaves. They also prefer fertile habitats.
Willis et al. 2010	Plants	Concord, Massachusetts, USA	×		×					IAS have a higher ability to adjust their flowering time in response to climate change than native species.
Yessoufou et al. 2014	Mammals	Alien species in South Africa	×		×					Evolutionary history influences invasion success.